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Demography of an invading forest insect reunited with hosts and parasitoids from its native range

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Abstract

The Sirex woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a widespread invasive pest of pines in the Southern Hemisphere, was first detected in North America in 2004. This study assessed the impacts of life history traits, host resistance and species interactions on the demography of *S. noctilio* in New York, Pennsylvania and Vermont, then compared key metrics to those found in the native range in Galicia, Spain. Many trees naturally attacked by *S. noctilio* in North America produced no adult woodwasps, with 5 of 38 infested trees (13%) sampled across six sites yielding 64% of emerging insects. Reproductive success was highest in the introduced host scots pine, *Pinus sylvestris*, but native red pine, *Pinus resinosa*, produced larger insects. *Sirex noctilio* required one or sometimes two years to develop and sex ratios were male biased, 1:2.98 ♀:♂. Body size and fecundity were highly variable, but generally lower than observed in non-native populations in the Southern Hemisphere. Hymenopteran parasitoids killed approximately 20% of *S. noctilio* larvae and 63% of emerging adults were colonized by the parasitic nematode *Deladenus siricidicola*, although no nematodes entered eggs. Demographic models suggested that *S. noctilio* in the northeastern USA have a higher potential for population growth than populations in the native range: estimated finite factor of increase, λ, was 4.17–4.52 (depending on tree species colonized), compared to $\lambda = 1.57$ in Spain.

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Keywords
Forest pest, invasive species, population ecology, *Sirex noctilio*, woodwasp

Introduction

Non-native insects are among the greatest current threats to global forest resources (Liebhold et al. 2017). Economic and ecological impacts in coming years are expected to be severe (Mack et al. 2000) as introduction rates increase with the intensification of human transport (Banks et al. 2015; Brockerhoff and Liebhold 2017). Despite efforts to develop tools that can identify important invasive species before they become established and spread (Roy et al. 2015; Matthews et al. 2017), anticipating the effects of invasions in new regions remains challenging (Simberloff et al. 2013). The difficulty of predicting future invasions is exacerbated by the fact that many organisms, whose presence goes largely unnoticed in some places, particularly within their native range, can become damaging pests in others.

One approach for identifying key drivers of impacts caused by alien species is to compare important demographic parameters across native and invaded ranges (Guo 2006; Broennimann and Guisan 2008; Ayres et al. 2014). Across disparate regions of a species' introduced range, population behavior may differ as a consequence of variation in key life history traits, population genetics or local adaptation, host identity, density and relative suitability, and/or the composition or abundance of key community members including mutualists, competitors and natural enemies, among other factors (Garnas et al. 2016). Identifying the demographic forces responsible for sometimes dramatic differences in pest abundance and aggressiveness is a difficult proposition.

The Sirex woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), provides an ideal system for the comparison of invasive behavior across a range of contexts, with native populations in Eurasia and widely-studied non-native populations in both the Northern and Southern Hemispheres (Slippers et al. 2015). *Sirex noctilio* is one of the most prominent agents of tree mortality in Southern Hemisphere pine plantations in Australasia (Carnegie and Bashford 2012), South Africa (Hurley et al. 2007) and South America (Lantschner and Corley 2015). Like many introduced forest pests and pathogens, this species has minimal impacts in its native range (Spradbery and Kirk 1981; Ayres et al. 2014). Superficially at least, North American *S. noctilio* population dynamics appear to more closely resemble native Eurasian populations than highly damaging Southern Hemisphere populations (Gilbert and Miller 1952; Haugen 1990; Hurley et al. 2007).

Sirex noctilio was first detected in North America in a survey trap in Fulton, NY near Lake Ontario in 2004 (Hoebeke et al. 2005) and surveys during the following two years confirmed the presence of reproducing populations in 17 Canadian and 27 US counties (Dodds et al. 2007; Dodds and de Groot 2012). The wasp has since spread northwards into Ontario and Quebec, Canada and southwards into at least eight US states. *Sirex noctilio* mainly colonizes and reproduces in a wide range of hard pine (subgenus *Pinus*) hosts, though other pines and conifers are occasionally utilized

(Hoebeke et al. 2005). The primary susceptible pine hosts in the current US range of *S. noctilio* are the native red pine *Pinus resinosa* Aiton and the introduced European Scots pine *P. sylvestris* L. Both occur in small, isolated stands in the northeastern USA, largely as a legacy of plantings carried out by the Civilian Conservation Corps (CCC) in the wake of the Great Depression (Maher 2008). Many such stands are even-aged and have been minimally managed following establishment. They are frequently overstocked, stressed and in poor condition (Dodds et al. 2010; Zylstra et al. 2010). These stands often contained dying trees even prior to *S. noctilio* invasion and have little or no timber value (Ayres et al. 2014). Although the native Eastern white pine *P. strobus* is abundant in this region and has been shown to be a suitable host for *S. noctilio* larvae, female woodwasps are rarely attracted to it and the species has not been meaningfully impacted (Haavik et al. 2017). For these reasons, economic losses associated with *S. noctilio* spread in eastern North America have been minimal (Ayres et al. 2014; Haavik et al. 2016; Haavik et al. 2018).

Female *S. noctilio* oviposit in suppressed or weakened pine trees (Dodds et al. 2010; Ayres et al. 2014). At each oviposition site, females drill one or more tunnels that branch from a single entrance through the bark (Madden 1974; Spradbery 1977). These wounds typically result in resin exudation and the drippings that form on the outside of the tree are used as an indicator of *S. noctilio* attacks during surveys (Ayres et al. 2009). Into each oviposition tunnel, gravid females then deposit one or more of the following: eggs, a phytotoxic venom (Madden 1968) and oidia (spores) of the obligate mutualist fungus *Amylostereum areolatum* (Fr.) Boiden (Russulales: Stereaceae) (Francke-Grosman 1939; Madden and Coutts 1979). If tree defenses are overcome, *A. areolatum* establishment and rapid tree decline normally follow (Coutts 1969; Neumann et al. 1987; Slippers et al. 2012). Larvae develop and pupate inside the xylem (Ryan and Hurley 2012), with the majority emerging after one year in most populations (but see Morgan 1968).

A similar natural enemy complex is found in both the native range of *S. noctilio* and in North America. In North America, several native parasitoid species utilize both *S. noctilio* and native siricid species, such as *S. nigricornis* (Coyle and Gandhi 2012). These include *Ibalia leucospoides ensiger* (Norton) (Hymenoptera: Ibaliidae), *Rhyssa persuasoria* (L.) and *R. lineolata* (Kirby) (Hurley et al. 2007; Slippers et al. 2015). The rhyssines can, in turn, be parasitized by the kleptoparasitoid *Pseudorhyssa* spp. (Couturier 1949; Spradbery 1969). The parasitic nematode *Deladenus* (= *Beddingia*) *siricidicola* (Tylenchida: Neotylenchidae) has a bicyclic life cycle, with a free-living asexual stage that feeds on *Amylostereum spp.* fungi within a tree and a parasitic sexual stage that occurs in the presence of developing siricids. The parasitic form is characterized by altered morphology and enters larvae and ultimately the testes or ovaries of the adult wasps, entering and sterilizing the eggs of females which vector them to new trees (Bedding 1967, 1972). *Deladenus siricidicola* strains in North America appear to be non-sterilizing, however, with nematodes reaching the gonadal tissues, but not entering the eggs (Kroll et al. 2013).

One possible explanation for differences in the behavior and impacts of invasive species populations is variability in important life history traits that impact potential

population growth via fitness and fecundity. Perhaps the most important of these are insect body size and sex ratio (Kajita and Evans 2010; Liu et al. 2017; Tabak et al. 2018). *Sirex noctilio* exhibits significant sexual dimorphism as well as an unusual degree of within-sex body size variation, with more than a 3-fold variation in female size reported in both Tasmania (Madden 1974) and Argentina (Corley et al. 2007). Sex ratio differences can also have profound effects on population demography and can influence outcomes of invasions (Xu et al. 2016), as well as their ecological consequences (Fryxell et al. 2015). *Sirex noctilio* sex ratios vary widely (Caetano and Hajek 2017), from relatively even (~ 1:3 ♀:♂) in the native range in Spain (Lombardero et al. 2016) to extreme male-biased populations (~ 1:32 ♀:♂) in Brazil (Iede et al. 1998). Since they are haplodiploid, unmated females produce exclusively male offspring via arrhenotoky (Gardner 2014). When males are scarce, such as in recently introduced or highly dispersed populations, sex ratios might be highly male-biased due to selective investment in sons (Queffelec et al. 2019) or lower mate-finding success among females.

Another potential explanation for variation in *S. noctilio* impacts is tree resistance or variation in the suitability of host trees, which has been hypothesized as a key factor controlling populations in North America (Haavik et al. 2017). This could differ as a function of species and provenance, planting density and management in plantation environments or stand density and history in the case of natural or semi-natural stands. This variation could be further mediated by environmental effects on plant investment in growth versus defense (Herms and Mattson 1992) or by genetic differences in susceptibility, attractiveness or suitability as a larval resource. If these factors lead to differences in host susceptibility between environments, both *S. noctilio* population behavior and tree mortality patterns would be impacted (Haavik et al. 2016a; Martinson et al. 2018). *Sirex noctilio* is known to mainly attack suppressed or weakened trees in its native range or when at sub-outbreak levels in invaded areas (Madden 1968). Early studies of *S. noctilio* outbreaks in New Zealand suggested that intermittent drought increased synchrony in the susceptibility of plantation trees and recent findings in Argentina support this hypothesis while further suggesting that drought-related impacts can vary dramatically among host tree species in a region (Lantschner and Corley 2015; Lantschner et al. 2019).

A third potential explanation for frequent *S. noctilio* outbreaks in certain environments is the lack of controls by natural enemies in some non-native populations (Keane and Crawley 2002; Boissin et al. 2012). Since the appearance of *S. noctilio* as a pest in the early 1900s in New Zealand, management efforts throughout its invaded range have been dominated by the development and adaptation of nematode-based biocontrol strategies (Hurley et al. 2007; Slippers et al. 2015). In Southern Hemisphere countries, both intentional (e.g., New Zealand, Australia, South Africa) and accidental (e.g., Argentina, Uruguay) release of hymenopteran parasitoids may help limit woodwasp populations (Fischbein and Corley 2014). Differences in parasitoids could contribute to differences in outbreak behavior among regions.

Our study was driven by the motivation to better understand current and potential future *S. noctilio* population dynamics in the eastern USA. Comprehensive research

efforts to date in the USA and Canada have generated a range of estimates for important demographic parameters in these expanding populations and we have summarized these estimates in Table 1. It nonetheless remains unclear which factors will most strongly influence the trajectory of *S. noctilio* populations. Whether the relatively low population densities, growth rates and impacts in North America will persist — particularly as ranges expand and new hosts are encountered — is an open question. In this study, we evaluated the relative influence of life history traits, interactions with natural enemies and host susceptibility on estimated *S. noctilio* population growth rates in the northeastern United States. We then compared these results to demographic analysis from a recent study in the native range in Galicia, Spain (Lombardero et al. 2016) in order to understand how woodwasp populations might be expected to behave in North American pine forests as *S. noctilio* range expansion continues.

Table 1. Life history parameters reported in previous studies in North America. Summary of findings to date from all North American studies that have assessed aspects of *Sirex noctilio* life history. Variables include timing of emergence, voltinism, sex ratio, body size, fecundity, parasitism and larval survivorship.

Variable	Value	Location	Source
Emergence timing	early July to early September	Ontario	Ryan et al. (2012)
	July to September	Ontario	Haavik et al. (2013)
	early July to early September	NY & PA	Foelker et al. (2016)
	June to October	NY & PA	Hajek et al. (2017)
	July to October	NY, PA, VT	This study
Development time	4.1% required more than 1 year	Ontario	Ryan et al. (2012)
	0.8% larvae remaining after year 1	central NY	Myers et al. (2014)
	4% larvae remaining after year 1	NY & PA	Foelker et al. (2016)
	1.5–26.7% required > 1 year	NY & PA	Hajek et al. (2017)
	10.4% required 2 years	NY, PA, VT	This study
Sex ratio	20.6% ♀	central NY	Long et al. (2009)
	~ 25% ♀	Ontario	Ryan et al. (2012)
	27% ♀	central NY	Myers et al. (2014)
	variable; 13.7% - > 60% ♀	Ontario	Haavik et al. (2016b)
	25% ♀	NY, PA, VT	This study
Body Size	pronotum width 3.2 mm (parasitized), 3.5 mm (non-parasitized)	NY & PA	Kroll et al. (2013)
	pronotum width ♀ 3.2 mm, ♂ 2.2 mm	Ontario	Haavik et al. (2016a)
	♀ prothorax 3.9 mm (non-parasitized)	NY & PA	Hajek et al. (2017)
	♀ body 19.7 mm; prothorax 2.6 mm; head capsule 2.8 mm	NY, PA, VT	This study
Fecundity	Average No. eggs: 79.6 (parasitized), 108.3 (non-parasitized)	NY&PA	Kroll et al. (2013)
	No. eggs = 69·(pronotum width in mm)-96	Ontario	Haavik et al. (2016a)
	No. eggs = 0.17·(body length in mm)$^{2.072}$	NY, PA, VT	This study
***Ibalia leucospoides* parasitism**	21%	central NY	Long et al. (2009)
	10.6% *P. sylvestris*, 10.8% *P. resinosa*	NY	Eager et al. (2011)
	20.8%	Ontario	Ryan et al. (2012)
	18%	central NY	Zylstra and Mastro (2012)
	3.4–17%	Ontario	Haavik et al. (2015)
	13%	NY & PA	Foelker et al. (2016)
	0–46%	Ontario	Haavik et al. (2016b)
	20%	NY, PA, VT	This study

Variable	Value	Location	Source
Rhyssine parasitism	1%	central NY	Long et al. (2009)
	4.4% *P. resinosa*, 8.3% *P. sylvestris*	NY	Eager et al. (2011)
	3%	Ontario	Ryan et al. (2012)
	10%	central NY	Zylstra and Mastro (2012)
	12%	NY & PA	Foelker et al. (2016)
	0–6%	Ontario	Haavik et al. (2016b)
	3.5%	NY, PA, VT	This study
Total hymenopteran parasitism	21.8%	Central NY	Long et al. (2009)
	16.4%	NY	Eager et al. (2011)
	23.4%	Ontario	Ryan et al. (2012)
	41.2%	NY & PA	Kroll et al. (2013)
	1–50% range	Ontario	Haavik et al. (2016b)
	23.4%	NY, PA, VT	This study
***Deladenus* parasitism**	38% of ♀, no sterilization	Ontario	Ryan et al. (2012)
	0.2–3% in larvae	central NY	Zylstra and Mastro (2012)
	27.9% all individuals	NY & PA	Kroll et al. (2013)
	23.7% all individuals	NY & PA	Foelker et al. (2016)
	32–64% of ♀, 23–62% of ♂	Ontario	Haavik et al. (2016a)
	23.6% of ♀; higher in *P. sylvestris* than *P. resinosa*	NY	Williams and Hajek (2017)
	62%	NY, PA, VT	This study
Survivorship (egg to adult)	~ 1–14% larval survivorship	Ontario	Haavik et al. (2015)
	30% larval mortality within tree	NY	Foelker (2016)
	~ 5%	Ontario	Haavik et al. (2017)
	28%	NY, PA, VT	This study

Materials and methods

Study area and materials

We collected *S. noctilio* in New York, Pennsylvania and Vermont in 2013, 2014 and 2015. We searched for stands of hard pines (*P. resinosa* and *P. sylvestris*) during spring and summer, noting the locations of trees with emergence holes and resin drippings indicating *S. noctilio* attack in the previous season. Trees attacked by *S. noctilio* were difficult to find, with > 80% of stands showing no signs of woodwasp presence. In total, we located active *S. noctilio* populations in six locations in New York (MF: Montour Falls, Schuyler County, 42.3354°N, 76.8138°W), Pennsylvania (DE: Delmar, Tioga County, 41.7209°N, 77.3772°W; MI: Middlebury, Tioga County, 41.8416°N, 77.4072°W, BL: State Game Lands 276 in Blacklick, Indiana County, 40.4886°N, 79.1070°W; CL: Clarion County, 41.1777°N, 79.2269°W) and Vermont (UN: Underhill, Chittenden County, 44.4847°N, 72.9656°W) across three years. As is common in the region, most sites primarily contained one tree species: three stands contained *P. sylvestris* only (MF, DE, MI), two stands contained *P. resinosa* only (BL, CL) and one stand contained both (UN), though *P. resinosa* was more abundant (Table 2). We recognize that species and site are necessarily confounded in this study due to the rarity of naturally-attacked hard pine stands on the landscape. We still chose to include comparisons of tree species in our analysis because each species occurred at multiple sites dispersed throughout the study area.

Table 2. Summary of trees and emerging insects sampled in each year of study. Number of trees sampled and number of native *Sirex nigricornis*, non-native *S. noctilio* and *Sirex spp.* parasitoids (*Ibalia leucospoides* and the rhyssines) collected from each tree species, at each site, across sampling years.

Year	State	County	No. trees	Tree Species	No. *Sirex noctilio*	No. *Sirex nigricornis*	No. *Ibalia leucospoides*	No. rhyssines
2013	NY	MF	3	*P. sylvestris*	1	0	0	0
	PA	DE	8	*P. sylvestris*	170	0	74	4
	PA	MI	3	*P. sylvestris*	0	0	0	0
	VT	UN	4	*P. resinosa*	71	68	0	30
2014	PA	DE	8	*P. sylvestris*	499	0	96	12
	VT	UN	1	*P. sylvestris*	2	9	0	1
	VT	UN	2	*P. resinosa*	77	66	2	16
2015	PA	BL	4	*P. resinosa*	41	0	0	0
	PA	CL	5	*P. resinosa*	130	0	67	3
Total			**38**		**991**	**143**	**239**	**66**

During late June or early July 2014–2016, we visited previously-identified sites to cut trees attacked in the prior season. All trees were dead or dying at the time of cutting. Over three years, we felled 38 attacked trees, recording GPS locations and diameter at breast height (dbh) for each. After felling, we cut each stem into ~ 1 m-long bolts, discarding the top of the tree (diameter < ~ 2 cm). Bolts were labeled individually to record their position relative to the ground and transported to emergence containers at Dartmouth College, Hanover, NH.

Insect emergence

Wasp-infested logs were placed in 55-gallon laminated cardboard emergence drums and stored indoors (ambient laboratory temperature ~ 21 °C). Drum openings were covered with fine mesh to prevent insect escape. Drums were checked every 1–3 days during peak emergence (mid-July to September) and at least twice a week thereafter until several weeks had passed with no new emergences (late October or early November). At the end of the first emergence season, we removed dead insects, then stored bolts in the laboratory until the following May, at which point we resumed regular checks. All emerging insects were collected, including *S. noctilio*, the native *S. nigricornis* and hymenopteran parasitoids. Due to low overall numbers, rhyssine parasitoids (*R. persuasoria* and *R. lineolata*) and kleptoparasitoids *Pseudorhyssa* spp. were combined for analysis and referred to as "rhyssines". For *S. noctilio* and *S. nigricornis*, we measured body length (excluding the ovipositor), then dissected each individual to check for nematodes. Nematodes from a subset of wasps were cultured and confirmed as *D. siricidicola* when they were sequenced as part of a study by Fitza et al. (2019). For 176 of the females, we counted the total number of eggs and, for 36 haphazardly selected individuals, we measured the length of five eggs per female using a compound microscope.

Bolt measurements and dissections

Collected bolts were weighed and measured for length and diameter at each end. For each bolt, we calculated the surface area and volume from length and diameter. Before we placed them in emergence drums, we measured wood moisture content at five locations along each bolt (~ 0.8 cm depth) using a Delmhorst RDM-3 moisture meter (Delmhorst Instrument Co., Towaco NJ) and averaged these measurements for analysis. Occasional measurements above or below the operating range of the device (6–60%) were recorded as 6% and 60%, respectively.

After insects finished emerging in the second year (at least two months with no further emergence), we dissected a subset of bolts (2–3 per tree). We counted resin drippings and emergence holes, then removed the bark and cambium to count oviposition sites (attacks) and the number of holes (drills) per attack using an illuminated tabletop magnifier (5×) and hand lens (10×–20×) as needed, following methods established by Lombardero et al. (2016). For each attack, we noted the presence or absence of lesions (Suppl. material 1: Figs S1, S2), which are thought to be indicative of a polyphenol defense response by the tree (Coutts and Dolezal 1966; Lombardero et al. 2016). Since lesions were assessed two years after bolts were collected and may have faded over time, we considered this to be a conservative estimate of lesion formation.

For each bolt, we estimated the number of eggs laid, based on the number of attacks and drills per attack following Madden (1974) and Haavik et al. (2015):

$$\#\ \text{eggs} = 0.01 \cdot \text{single drills} + 0.68 \cdot \text{double drills} + 1.55 \cdot \text{triple drills} + 2.22 \cdot \text{quadruple drills}$$

After dissection, we cut each bolt into three equal lengths (avoiding knots) to expose fresh surfaces. We estimated the percentage of the cross-sectional area colonized by bluestain (ophiostomatoid) fungi by outlining visible bluestain on the cut surface of each bolt and photographing the surface (see Suppl. material 1: Fig. S2). Area quantification was performed using ImageJ as described in Lombardero et al. (2016).

Additional data

For analyses of *S. noctilio* body size, egg number and allometric equation development, we incorporated additional data from 1,511 emerging *S. noctilio*, collected from 53 trees sampled in central NY in 2008; hereafter referred to as the "Central NY data set" (see Zylstra et al. (2010) and Myers et al. (2014) for protocol details). These trees were chemically girdled in 2007 and felled after the oviposition season finished, at which point they were transported to the USDA APHIS PPQ laboratory (North Syracuse, NY) for storage in emergence barrels. Emerging insects were collected and the following measurements were recorded: hind tibial length, prothorax width, mass and egg count. As these trees were chemically girdled rather than naturally attacked, analyses were done separately from 2013–2015 data.

To compare egg sizes between the USA and Spain, we also measured eggs from *S. noctilio* collected emerging from bolts in Galicia, Spain in 2013–2015, as described in Lombardero et al. (2016). To further compare demographic patterns between the USA and Spain, we reanalyzed data used to build Table 1 in Lombardero et al. (2016), reproducing some parts of that Table and updating it with additional calculations of numbers of eggs laid, based on published estimates (Madden 1974) as described above.

Statistical analysis

Data analysis was conducted in JMP Pro 13.0 (SAS Institute 2016) and R Version 3.4.3 (R Core Team 2017). All means are reported with standard errors (SE) unless otherwise noted. In cases of unequal variance, we used Welch's Test to compare means. As we did not sample at all sites in all years, we included a composite variable Site-Year in some analyses.

We used Maximum Likelihood to estimate the number of wasps emerging per tree, number of insects emerging per bolt and the number of nematodes per parasitized *S. noctilio* adult. For each of these metrics, we evaluated four candidate distributions and compared them via log-likelihood: Poisson, zero-inflated Poisson, negative binomial and zero-inflated negative binomial (R package VGAM; Yee 2015).

We used Chi-square statistics to test for differences in: voltinism between male and female wasps; sex ratio between pine species and across sites; and nematode parasitism among tree species, sites and wasps of different sexes. We used restricted Maximum Likelihood generalized linear mixed models (R package lme4; Bates et al. 2015) to examine relationships between predictors of interest and emergence date, body size and egg length. We calculated *P* values using the Satterthwaite approximation for degrees of freedom (package lmerTest; Kuznetsova et al. 2017) and selected the best models by comparing AIC values (AICtab in bbmle package; Bolker et al. 2017) unless otherwise noted in results.

We used simple linear regression to test for a relationship between emergence date and body size, analyzing insects emerging from the *P. resinosa* and *P. sylvestris* separately. The impacts of sex and tree species on insect body size were examined using 2-way ANOVA with an interaction term. To describe the relationship between body size and *S. noctilio* egg number, we used the nls function in the R base package to fit a power function to our egg count data from dissected females, then tested for effects of tree species and voltinism on egg number by analyzing the residuals.

Parasitism rates were estimated as the slope of the regression line (with forced intercept = 0) of numbers of emerging parasitoids versus numbers of all emerging insects (siricids plus parasitoids) (Cochran 1977). We then used multiple regression to assess the effect of tree species on parasitism rate.

To examine relationships between bolt traits and measures of insect attack and emergence, we generated a matrix of Pearson Correlation Coefficients using all complete pairwise observations, then visualized them with the R package corrplot (Wei and Simko 2017) using an $\alpha = 0.05$ significance level. We transformed variables as noted

to address departures from normality and heterogeneity of variance. The logit transformations used a standard adjustment (Warton and Hui 2011) of 0.025 (R package CAR; Fox and Weisberg 2011). Patterns in drills per attack were assessed using a generalized linear mixed model with a Poisson link function, that included random effects of tree (nested within site) and bolt (nested within tree). We estimated emergence per attack and emergence per egg as the slope of a regression (with forced intercept = 0) of these pairs of variables (Cochran 1977).

Results

Sirex life history in NY,VT and PA

We collected 1007 *S. noctilio* (253 females and 754 males) over three years from 38 trees harvested in New York, Pennsylvania and Vermont (Table 2). The majority of *S. noctilio* emergence was concentrated in a small number of trees, with production per tree best described by a zero-inflated negative binomial (ZINB) distribution with $\Phi = 0.32$ (proportion of excess zeroes), $\mu = 75.39$ and overdispersion parameter $k = 0.35$ (Suppl. material 1: Fig. S3). Most wasps (89.6%) emerged within one year of bolt collection; the rest (10.4%) emerged in year two. Females were more likely than males to emerge in year 2 (21.7% vs. 6.6%; $\chi^2 = 40.53$, df = 1, $p < 0.0001$). Woodwasps emerged from 3 July to 2 November (Julian Days 184–306). This timing did not vary across years, but peak emergence date was slightly earlier for males than for females ($F_{1,839} = 3.74$, $p = 0.053$). Approximately 77% of the variation in emergence dates was among trees within a site.

The sex ratio of emerging *S. noctilio* was male biased 1:2.98 ♀:♂. Voltinism influenced sex ratios, with insects emerging in one year having a sex ratio of 1:3.5 ♀:♂ and females dominating in year 2, with 1:0.90 ♀:♂. Sex ratio also varied across sites, with the lowest proportion of males in a *P. resinosa* stand (Blacklick, Pennsylvania) and the highest at a *P. sylvestris* stand (Delmar, Pennsylvania; 0.32 vs. 0.83; $\chi^2 = 59.43$, df = 4, $p < 0.0001$). Although both of these sites are in Pennsylvania, the time since the stands had first become infested appeared to differ: *S. noctilio* had likely recently arrived to Blacklick, while a population was established in the area around Delmar since at least 2008 (Williams and Hajek 2017).

Sirex noctilio body length ranged from 6–37 mm, with an average length of 15.66 ± 0.16 mm. Females ($n = 251$, 19.67 ± 0.31 mm) were larger than males ($n = 752$, 14.32 ± 0.15 mm) ($t = 15.40$, df = 369.63, $p < 0.0001$; Fig. 1) and insects emerging in the second year were larger than those emerging in the first ($F_{1,860.69} = 12.41$, $p < 0.001$). Year of emergence effects were consistent across sexes but more pronounced for males (1st year: 14.08 ± 0.15 mm vs. 2nd year: 17.83 ± 0.62 mm; $t = 5.92$, df = 52.71, $p < 0.0001$) than for females (1st year: 19.4 ± 0.37 mm vs. 2nd year: 20.65 ± 0.56 mm; $t = 1.66$, df = 104.83, $p = 0.03$). In the Central NY data set, females ranged from 10–35.5 mm and were larger than males (23.64 ± 0.25 mm vs. 16.95 ± 0.12 mm;

$F_{1,1500} = 239.38$, $p < 0.0001$). Allometric relationships between body size measurements (length, width of head capsule and mass) for insects in the Central NY data set are included in Suppl. material 1 (Suppl. material 1: Fig. S4).

Number of eggs per female ranged from 5 to 284. Number of eggs was positively related to body size and well described by a power function where number of eggs = $0.17 \cdot (\text{BodyLength})^{2.072}$ (Fig. 2). Analysis of residuals from the fitted power function showed no effect of tree species or voltinism on number of eggs ($F_{3,141} = 0.31$, $p = 0.82$). Egg lengths ranged from 0.99–1.51 mm with an average of 1.26 ± 0.01 mm. We found no difference in egg size between Spain and the USA ($t = 0.48$, df = 21.99,

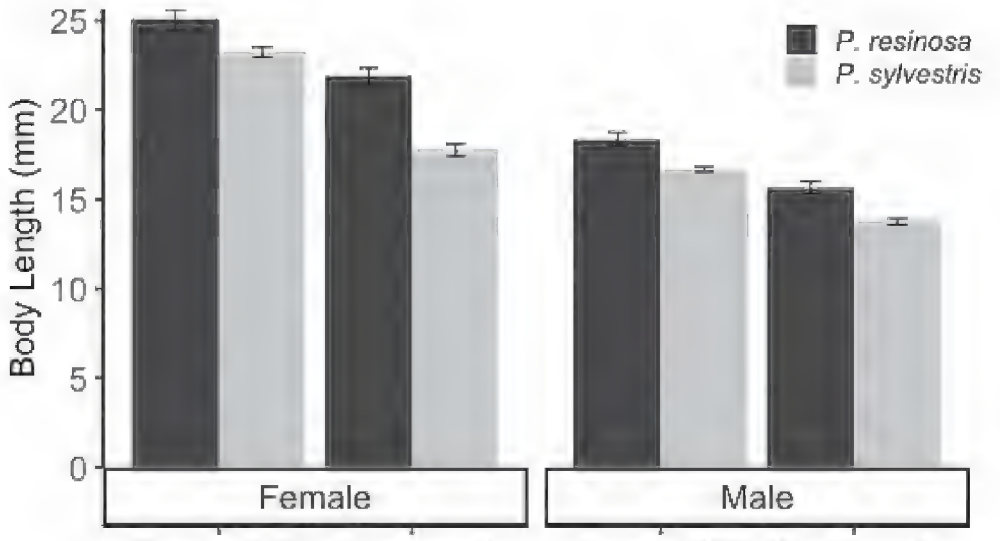

Figure 1. Body size variation in *Sirex noctilio*. Females were larger than males and insects emerging from *Pinus resinosa* were larger than those emerging from *P. sylvestris* (Central NY and Northeast data sets plotted separately). Bars show mean ± SE.

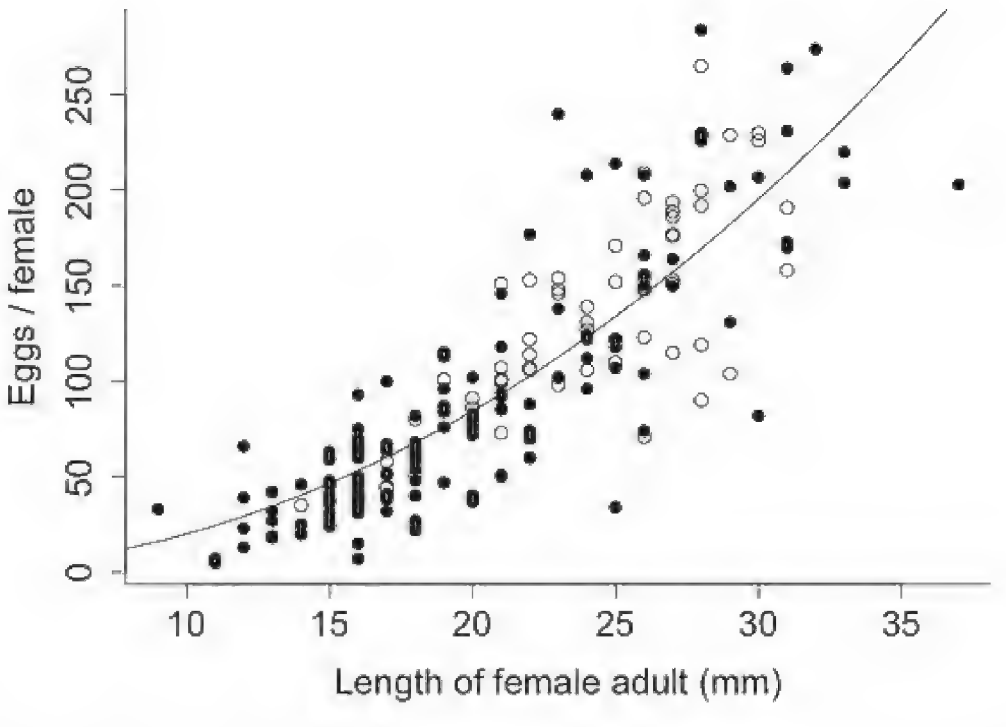

Figure 2. Relationship between body size and fecundity. Number of eggs (y) increases with female *Sirex noctilio* body size at the same rate for the main data set (closed circles) and Central NY data set (open circles). Line is fitted power function $y = 0.17x^{2.072}$ for the combined data set.

p = 0.64). There was some variation in egg size among wasps, but very little variation among eggs produced by each individual (estimated variation due to random effect in mixed model = 68 and 0%, respectively).

Host suitability and attack behavior

Dissection of 76 bolts from 24 trees (10 *P. radiata* and 14 *P. sylvestris*) yielded 11,253 attacks comprising 16,604 oviposition drill holes. Attack density was higher in *P. sylvestris* than in *P. resinosa* (8.83 ± 1.29 vs. 5.28 ± 1.72 attacks/dm^2; $F_{1,51.72}$ = 4.43, p = 0.04). The number of drills per attack ranged from 1 to 6, distributed as follows: 64% were single drills, 27% doubles, 8% triples and 1% four or more. The number of drills per attack was slightly higher on average for *P. resinos*a (1.62 ± 0.01) than for *P. sylvestris* (1.38 ± 0.01) (Fig. 3; n = 11,253, z = -2.21, p = 0.03). The estimated variation in drill count per attack among bolts (nested within tree) and among trees (nested within site), was low (< 10% of the total random variation for each).

Emergence of adult wasps was concentrated in a relatively small number of bolts and was best described by a zero-inflated negative binomial (ZINB) distribution with parameters Φ = 0.24, μ = 20.43 and k = 0.85. For both tree species, emergence was — as expected — positively correlated (r = 0.36 - 0.79) with attacks, attack density, drills, drill density, drills per attack, estimated number of eggs laid and the estimated density of eggs laid, most of which were correlated with each other (Suppl. material 1: Table S1). In *P. sylvestris*, but not *P. resinosa*, variables associated with oviposition (estimated eggs laid, egg density), emergence per egg and total emergence were negatively correlated with bolt moisture, bluestain presence and lesion formation in response to attack (Suppl. material 1: Table S1). Lesion formation was positively correlated with bolt moisture level (r = 0.72) in *P. sylvestris* only. The percentage cross-sectional area of

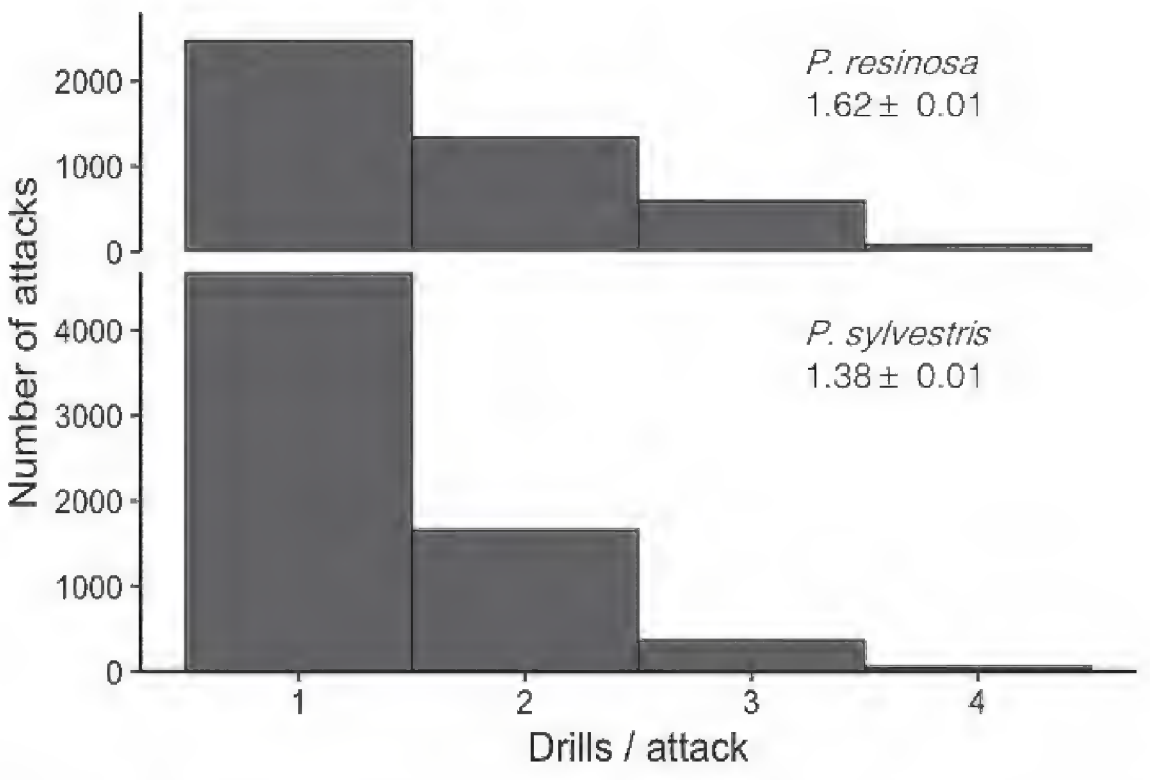

Figure 3. Number of drills per attack across sampled tree species. *Sirex noctilio* attacks (oviposition sites) with 1, 2, 3 or 4+ drill holes for *Pinus sylvestris* and *P. resinosa*.

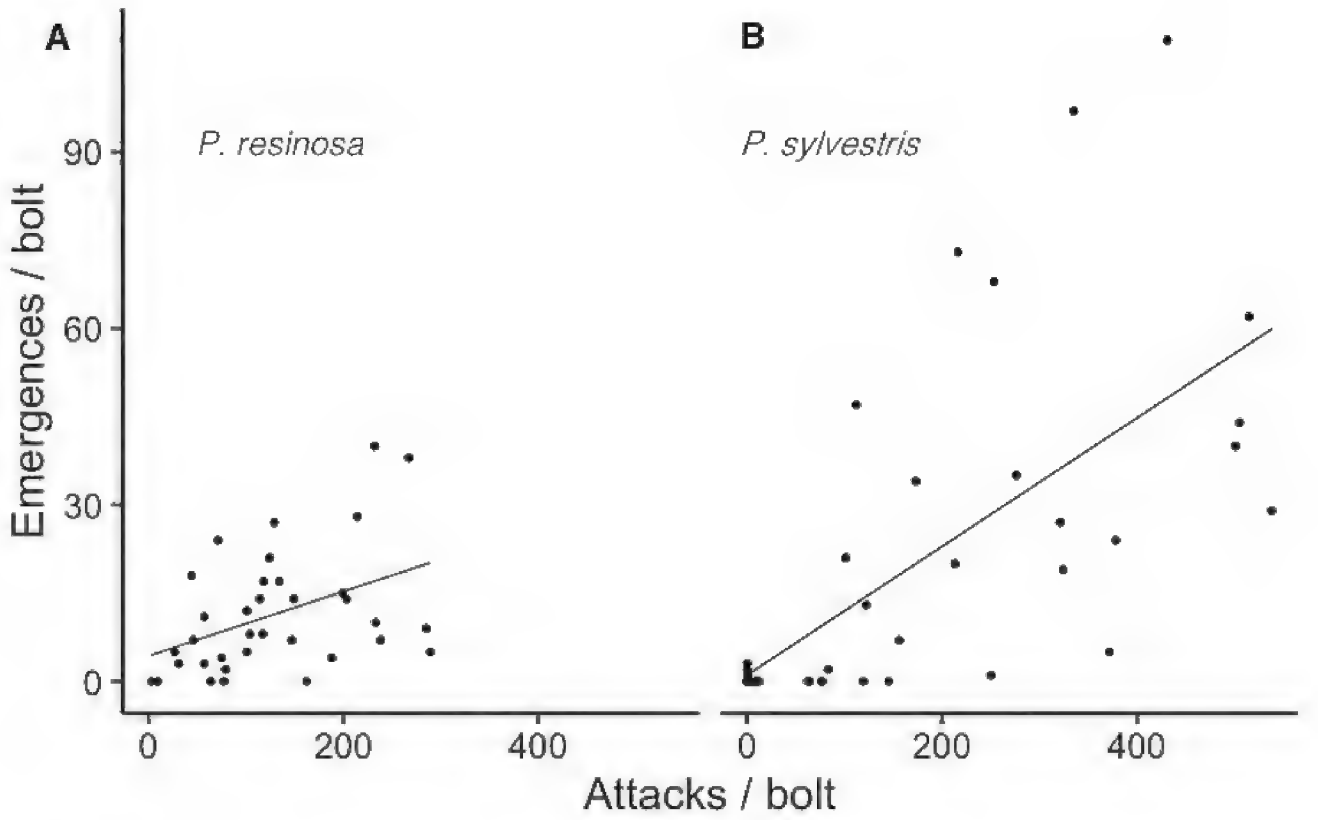

Figure 4. *Sirex noctilio* emergence success. Emergence per attack for *Pinus resinosa* (**A** slope = 0.08 ± 0.01) and *P. sylvestris* (**B** slope = 0.11 ± 0.01) and emergence per estimated number of eggs laid for *P. resinosa* (**C** slope = 0.16 ± 0.02) and *P. sylvestris* (**D** slope = 0.41 ± 0.04). Each point represents one bolt.

bluestain per bolt was positively correlated with both bolt moisture content and bolt volume (Suppl. material 1: Table S1).

Emergence per attack was higher for *P. sylvestris* (0.11 ± 0.01) than *P. resinosa* (0.08 ± 0.01) (Fig. 4); 63.8% of the *S. noctilio* produced came from the five trees that produced the most insects and these were all *P. sylvestris*. The proportion of emerging wasps that were male was higher for *P. sylvestris* (0.80) than for *P. resinosa* (0.64) (χ^2 = 28.60, df = 1, $p < 0.0001$). Insects emerging from *P. resinosa* were larger than those

emerging from *P. sylvestris* (Fig. 1; Northeast data set: $F_{1,32.98} = 4.95$, $p = 0.03$, Central NY data set: $F_{1,1500} = 29.61$, $p < 0.0001$) and the body size difference between males and females was more pronounced in *P. resinosa* than in *P. sylvestris* (Northeast only: $F_{1,974.24} = 8.85$, $p = 0.003$). Variation among trees within species accounted for 32% of the total random variation in adult size.

Species interactions

A total of 143 native *S. nigricornis* co-occurred with *S. noctilio* in our trees, but emergence of this native siricid was concentrated in three trees from one site (Table 2; Suppl. material 1). Hymenopteran parasitoids were abundant: we collected a total of 245 *Ibalia leucospoides* and 67 rhyssines (27 females and 40 males). Across all sites and years, total hymenopteran parasitism was 23.4 ± 2.0%, with no difference between *P. resinosa* and *P. sylvestris*. *Ibalia leucospoides* parasitized 20 ± 2.0% of *S. noctilio* larvae, with no difference between tree species. The percentage of *S. noctilio* parasitized by *I. leucospoides* increased with total emergence in *P. resinosa* ($F_{1,11} = 5.11$, $p = 0.04$), but not in *P. sylvestris*. Rhyssine parasitism was 3.5 ± 1.0% overall and was higher in *P. resinosa* (9.22 ± 2.0%) than in *P. sylvestris* (1.72 ± 0.30%; $F_{1,34} = 15.57$, $p < 0.001$).

Of the 806 *S. noctilio* assessed for nematode parasitism, 62% contained nematodes in gonadal tissue, with no difference between sexes ($\chi^2 = 0.25$, df = 1, $p = 0.62$). We found no instances of nematodes within *S. noctilio* eggs. Wasps emerging in the first year were more likely to be parasitized (63.52%) than those emerging in year two (13.64%) ($\chi^2 = 22.64$, df = 1, $p < 0.0001$). Among wasps emerging in year one, non-parasitized females were larger than parasitized females (22.03 ± 0.62 mm vs. 17.60 ± 0.49 mm; $t = 5.58$, df = 158, $p < 0.0001$) with the same pattern seen in males ($t = 4.75$, df = 644, $p < 0.0001$). Females also had smaller eggs in the presence of nematodes ($t = 3.17$, df = 21.98, $p = 0.004$). Adult woodwasps that emerged from *P. sylvestris* were much more likely to be parasitized by *D. siricidicola* than those that emerged from *P. resinosa* (81.3% vs. 5.15%; $\chi^2 = 363.85$, df = 1, $p < 0.0001$), but species and location were confounded (Table 2), so this finding could simply indicate spatial patchiness in nematode abundance. Estimates of nematode load per parasitized wasp ranged from 11 to 3,000 – the distribution of these values was best described by a negative binomial distribution with parameters $\mu = 395.2$ and $k = 1.04$. We found many wasps with < 500 nematodes and a few wasps with estimated parasite loads of up to ~ 2,000 or greater.

Reproductive potential

We constructed simple demographic models of *S. noctilio* in the northeastern USA, reporting study-wide values in addition to separate values for insects colonizing the two pine species in the study, *P. resinosa* and *P. sylvestris* (Table 3). An average-sized female of *S. noctilio* was predicted to contain 78 eggs (~ 66 eggs when emerging from *P. sylvestris* or 102 eggs when emerging from *P. resinosa*), based on body size-fecundity relationships. Nematodes did not enter *S. noctilio* eggs, so they had no direct impact on

Table 3. Demographic parameters for *Sirex noctilio* in Spain and the USA. Overall values for North America are shown, as well as separate values for *Pinus resinosa* and *P. sylvestris*. All data from Spain come from *P. pinaster*. Percent change in lambda (% Δ λ) is the percent change in USA λ when the Spain value for each row is substituted for the USA value. It indicates the relative impact of each of demographic factor on λ. Spanish values are adapted from Table 1 in Lombardero et al. (2016), with modifications to eggs/♀[1] and emergences/egg[2] as described in Methods.

	Spain	**North America**		**North America by Species**			
				P. resinosa		***P. sylvestris***	
	Parameter	**Parameter**	**% Δ λ**	**Parameter**	**% Δ λ**	**Parameter**	**% Δ λ**
Eggs/♀[1]	58	78	-26	102	-43	66	-12
Nematode escape	0.64	1	-36	1	-36	1	-36
Emergence/viable egg[2]	0.2	0.28	-28	0.16	27	0.41	-51
Hymenopteran escape	0.8	0.77	4	0.77	4	0.77	4
Proportion female	0.26	0.25	4	0.36	-28	0.2	30
♀/♀ (λ)	**1.57**	**4.20**	-63	**4.52**	-65	**4.17**	-62

[1]eggs/female calculated as the number of eggs expected in an average sized (20 mm) female; [2]calculated, based on egg estimates in Madden (1974).

egg viability. Estimated emergence per egg was higher for *P. sylvestris* than for *P. resinosa* (0.41 ± 0.04 vs. 0.16 ± 0.02; Fig. 4), with an average of 0.28 ± 0.03 overall. From the combination of differences in fecundity and emergence per egg, we estimated 16 and 27 larval progeny per female adult for *P. resinosa* and *P. sylvestris*, respectively. A hymenopteran parasitism rate of 23.4%, consistent across tree species, further reduced estimated emergence to 13 and 21 adult progeny per female, of which 36% and 20% were female (Table 3). Thus, the estimated maximum number of females per female per year (λ) was about 4.2 for the overall population or 4.52 and 4.17 for *P. resinosa* and *P. sylvestris*, respectively.

Discussion

Life history traits

Non-native *S. noctilio* populations in North America showed a higher potential for population growth than native populations in Galicia, Spain (Table 3), with $\lambda > 4$ vs. 1.57. This was driven by the absence of sterilization by nematodes in North America and notable differences in fecundity and larval survival inside host trees. Despite this higher potential for population growth, trees with *S. noctilio* were rare in North America and stems with signs of *S. noctilio* attack often failed to produce adult progeny. Over 64% of *S. noctilio* in this study came from 13% of sampled trees, similar to findings from Foelker (2016), where 53.5% of *S. noctilio* emerged from 16% of sampled trees. Williams and Hajek (2017) and Haavik et al. (2018) also recorded wide variation in emergence and frequent failure of *S. noctilio* reproduction in attacked trees. Similarly, 32% of trees in this study had no insect emergence, compared to 41% in the native

range in Galicia, Spain (Lombardero et al. 2016). Despite increased sampling effort, Lombardero et al. (2016) collected only 313 adults from 134 trees compared to our 1007 from 38 trees.

Our results broaden the evidence of remarkably high body size variation for *S. noctilio*, consistent with reports of an 8–38 mm range in length from the native range (Lombardero et al. 2016). When compared to other insect species known to have high size variability, female *S. noctilio* showed roughly twice as much variation (over 4.1× versus 2.1× in the next most variable species; Suppl. material 1: Table S2). This is surprising given the clear link between body size and fecundity (Honěk 1993), although Madden and Coutts (1979) hypothesized that adult size variation is determined by nutrition and the success of the mutualist fungus *A. areolatum* and other recent studies have supported the hypothesis that highly variable environmental or nutritional factors help determine adult body size (Foelker and Hofstetter 2014; González et al. 2014). This is also consistent with recent findings by Garnas et al. (2020), where a complex interplay of factors related to resource quality influenced woodwasp body size, even within a single tree. Although *P. resinosa* produced fewer *S. noctilio* individuals, they were ~ 23% larger than those produced in *P. sylvestris*, suggesting that *P. resinosa* is an attractive host, but may have higher host resistance to *S. noctilio*. When oviposition is successful, *P. resinosa* provides a suitable and perhaps superior substrate for *A. areolatum* growth and *S. noctilio* maturation.

High variation in woodwasp body size could also reflect genetic differences among wasps and complex selective landscapes that favor large insects in some instances, but not in others. Long feeding galleries necessary to produce large adults may be more feasible in large trees than small trees. Large males may have difficulties mating with small females (Caetano and Hajek 2017) and large adults of either sex may be more vulnerable to predators. The large size of female *S. noctilio* relative to males suggests the effect of natural selection on female size (likely favoring higher fecundity) is considerably stronger than natural or sexual selection on males (Wiklund and Karlsson 1988).

The fecundity of North American *S. noctilio* is higher than in Spain, but this is not driven by differences in body size. An average-sized female in our sample (19.67 mm long) had ~ 78 eggs. Although Spanish *S. noctilio*, measured by Lombardero et al. (2016), had a similar range in egg number (0 to 270 eggs per female), 19.7-mm females in Galicia, Spain were estimated to have ~ 56 eggs. Other North American studies also show elevated *S. noctilio* fecundity compared to native populations (Table 1). On the other hand, fecundity in this study was lower than that reported for Southern Hemisphere populations (e.g., 50–500 in New Zealand; Zondag and Nuttall 1977). The higher fecundity of *S. noctilio* in the Southern Hemisphere may be attributable to larger average body size, which has been widely reported (e.g., 24–32 mm average body size for females in South Africa; Hurley et al. 2008).

At a population level, observed male-biased sex ratios were similar to those previously reported in North America (see Table 1) and in the native range in Galicia, Spain (Lombardero et al. 2016). In this study, spatial patterns in North American sex ratios were opposite of what would be expected if the male bias were due to low mating success at the range edge since the lowest proportion of males was in the

most recently invaded region (Blacklick in central Pennsylvania) where attack densities were low. However, sex ratio has been found to vary widely among sites in other studies (e.g., Haavik et al. 2018) and has the potential to influence local or regional outbreak patterns.

Host selection and resistance

Host choice and oviposition behavior influence the success of *S. noctilio* in new landscapes. In our study, 64% of total attacks involved only a single drill. Single drills are thought to indicate rejection of the oviposition site (since eggs are rarely placed), perhaps as a consequence of the detection of suboptimal moisture levels and/or oleoresin pressure for fungal establishment, egg survival or larval success (Ryan and Hurley 2012; Hayes et al. 2015). Attacks with two or more drills normally contain eggs, as well as fungi and venom (Madden 1974). In Spain, only 43% of total attacks involved a single drill and, in Argentina, only 39% had one drill (Martinson et al. 2018). Evidently, the US stands in this study included a higher proportion of trees that were judged as low quality by ovipositing females. This may be due, in part, to rejection of trees with higher moisture content (Suppl. material 1: Table S1), variable host species attractiveness and differences in biotic and abiotic drivers of tree stress in different regions (Madden 1988; Haavik et al. 2017; Corley et al. 2018). Any factors that reduce host attractiveness and, thus, oviposition by female woodwasps have the potential to suppress population growth that can lead to outbreaks.

The fate of larvae inside host trees strongly influenced reproductive potential in both US and Spanish *S. noctilio* populations. This is consistent with past studies that have highlighted the role of host resistance in limiting *S. noctilio* reproduction and spread (Haavik et al. 2017; Haavik et al. 2018). Mortality at the egg and larval stages consistently reduced numbers of female offspring by over 70% (Table 3, Lombardero et al. 2016) and our finding of much higher reproductive success in *P. sylvestris* than in *P. resinosa* further highlights the potential for tree-specific factors to heavily influence *S. noctilio* population dynamics. However, other demographic factors also matter. For example, the lower survival of larvae feeding in *P. resinosa* vs. *P. sylvestris* was almost completely compensated by larger adult size (and, therefore, higher fecundity) and a higher proportion of females (Table 3). In the northeastern United States, small localized outbreaks have occurred, but tended to decline after several years as susceptible host trees were depleted. The potential for woodwasp population growth has probably been highly constrained in the Northeast by the limited availability of suppressed trees within stands of hard pines which are themselves rare in the landscape (Haavik et al. 2016).

Top-down controls on *S. noctilio*

Spanish woodwasp populations experience consistent top-down control by nematodes via sterilization of ~ 90% of the eggs in 39% of females (Lombardero et al. 2016). In contrast, sterilization of eggs by parasitic nematodes was absent in our US study popu-

lations. Although we found nematodes in ~ 63% of wasps sampled, they were only present in the body cavity, not within the eggs. Previous North American studies have also reported that *D. siricidicola* fail to sterilize *S. noctilio* eggs (but see Kroll et al. 2013 and Williams and Hajek 2017 for minor exceptions). Nematode impacts on reproductive potential in the region are, therefore, indirect, but may still be consequential: parasitized females in North America were smaller and less fecund than unparasitized females (17.6 mm and ~ 65 eggs vs. 22.0 mm and ~ 103 eggs). If nematode parasitism reduces adult body size, this corresponds to a 37% drop in the reproductive potential (λ) for parasitized vs. unparasitized females.

Our finding that nematode parasitism dropped to under 14% for larvae that took two years to develop supports the hypothesis that delayed development can help woodwasps evade parasitism (Corley and Bruzzone 2009). The incidence of nematode parasitism was also clumped (better fit by a negative binomial than a Poisson distribution; Vale et al. 2013). Presumably the patchy dispersion of nematodes reflects variation among trees in the introduction of nematodes by ovipositing woodwasps, in the establishment of *A. areolatum* on which the nematodes feed, and perhaps in the relative timing of wasp and nematode development, which must be synchronized for nematodes to effectively disperse inside emerging woodwasp adults. Even in Southern Hemisphere plantations where *D. siricidicola* is deployed for biological control, parasitism rates vary widely (Slippers et al. 2012) and annual augmentative releases are regularly practiced and typically necessary for effective control.

Hymenopteran parasitoids exerted a moderate top-down influence on North America *S. noctilio*, reducing the number of progeny by ~ 20%, which is within the range of reports from other studies in North America (~ 1–50%; Table 1) and the native range. In the most robust study of *S. noctilio* parasitoid complexes in North America to date, Foelker et al. (2016) found similar overall rates of hymenopteran parasitism (27.6% and 20.9% in 2010 and 2011). We found evidence of density-dependent effects from *I. leucospoides* at the tree level in *P. resinosa*. Similarly, Haavik et al. (2016b) found that *I. leucospoides* presence in Ontario was positively correlated with the density of attacked pines within stands. *Ibalia leucospoides* uses olfactory cues to locate *S. noctilio* oviposition sites, based on the presence of volatiles from the woodwasp mutualist *A. areolatum* (Martínez et al. 2006) and may detect resource-rich patches from some distance (Fischbein et al. 2012). A Type III functional response to *S. noctilio* presence has also been reported for hymenopteran parasitoids in Argentina, with attack rate increasing as the availability of *S. noctilio* oviposition sites increases (Fernández-Arhex and Corley 2005). At high *S. noctilio* densities, this parasitoid can help to suppress outbreaks. However, even if our highest *I. leucospoides* parasitism rate (33%) was found across all sites, this would only decrease lambda for *S. noctilio* in the northeastern USA by ~ 17% (Table 3). We suspect that the extreme patchiness of *S. noctilio* resources in the current North American range, combined with the solitary lifestyle and life history of *I. leucospoides* (Haavik et al. 2015), limits the potential for population regulation by these parasitoids.

Future *S. noctilio* expansion in North America

The presence of native pines, native siricids and native siricid parasitoids in North America may confer some biotic resistance to invasion by *S. noctilio* (Foelker 2016; Nunez-Mir et al. 2017). This differs from the Southern Hemisphere where neither pines nor their associates are native. Despite the similarities to the native range, our demographic analysis suggests higher population growth potential in North America vs. Spain (Table 3). This may result in complex dynamics if the woodwasp reaches native pine forests that are overstocked or experience frequent drought stress, attack by other pests and pathogens or wildfire (Adams et al. 2010; Anderegg et al. 2015). Interactions with other insects will also help shape these dynamics. Our study did not attempt to quantify competition, but we did see reduced *S. noctilio* emergence in the presence of bluestain fungi associated with bark beetle colonization. This is consistent with other studies where co-occurrence with other subcortical insects has been shown to reduce the reproductive success of *S. noctilio*, likely mediated by competition among fungal associates (Ryan et al. 2012). These fungal interactions also have the potential to influence woodwasp-nematode interactions and were found to reduce the survival of *B. siricidicola* and, thus, the effectiveness of biological control efforts, in Australia (Yousuf et al. 2014).

All hard pine species in North America are potentially susceptible to *S. noctilio* (Dodds and de Groot 2012). Populations in Michigan and southern Ontario colonize *P. banksiana* and will continue to encounter this host as they spread into new regions. Woodwasps expanding southwards will soon encounter southern pines including *P. palustris*, *P. taeda* and *P. elliottii* and establishment in western North America would permit colonization of lodgepole pine, *P. contorta*, which has been shown to be highly susceptible to outbreaks in Argentine Patagonia (Lantschner and Corley 2015). More comprehensive knowledge of variation among pine species in susceptibility to *S. noctilio* would help managers anticipate future impacts in North America.

More broadly, a comprehensive comparison of the population demography of Northern and Southern Hemisphere *S. noctilio* would help us better elucidate the importance of specific controls on *S. noctilio* populations and improve understanding of variable tree species susceptibility. Such studies would also help clarify the importance of landscape-level patterns in resource availability in determining woodwasp population growth rates. Current and future population models would also be improved by better understanding and incorporating density-dependent feedbacks in the demographics.

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Supplementary material 1

Tables S1, S2, Figures S1–S4

Authors: Flora E. Krivak-Tetley, Jenna Sullivan-Stack, Jeff R. Garnas, Kelley E. Zylstra, Lars-Olaf Höger, María J. Lombardero, Andrew M. Liebhold, Matthew P. Ayres

Data type: Text, tables and figures (docx. file)

Explanation note: This file includes demographic data from native *Sirex nigricornis* woodwasps that were collected during our study. Table S1. Correlation matrix of bolt-level variables for *P. resinosa* and *P. sylvestris*. Table S2. Review of 10th and 90th percentile female body mass from insect species estimated from source paper cited, showing comparatively higher female *S. noctilio* body size variation. Figure S1. Examples of *S. noctilio* oviposition sites, lesion formation and emergence holes in the field. Figure S2. Top panels show a typical bolt from *P. sylvestris* with bark removed and *S. noctilio* emergence holes and oviposition sites identified. Figure S3. The number of *S. noctilio* emerging per tree was best described by a zero inflated negative binomial distribution (dotted line) with proportion of excess zeroes $\Phi = 0.32$, $\mu = 75.39$ and overdispersion parameter $k = 0.35$. Figure S4. Allometric relationships for *S. noctilio* in the Central NY data set: number of eggs and adult female mass (a; quantile regression), adult female mass and adult female length (b; fitted power function) and adult length and width of adult head capsule (c; linear regression).

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